ECOLOGY OF COLLEMBOLA

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1. Introduction

It is not possible in a short rewiew of this kind to discuss in detail all aspects of Collembolan ecology. I should like to concentrate on certain aspects, in particular the relationship between autecological studies and synecology of Collembola, which may elucidate some of the currently held opinions in the older literature hintherto unexplained and shed new light on the most recent literature.

Some more or less comprehensive reviews on ecology and ecophysiology of Collembola were published recently (Joose 1983, Dunger 1983) and it is not necessary to repeat here their content. Autecological research on soil animals, including Collembola, concertrated mainly on ecophysiology in last decade (cf Vannier 1983). Some of the results obtained in the laboratory were verified by field experimentation. This should be a requirement for all ecological studies. Here some suggestions for further research are given.

2. Autecology

2.1. Humudity

Collembola live in wet as well as in dry ecosystems. But normally densities and species richness are greatest in humid and mesic environments. Collembola were originally both epigeic and soil inhabiting animals and some of them developed, during their phylogeny, strategies and adaptations to cope with water defficiency. Certain epigeic and atmobiotic species here cuticular structures which protect them against water loss (Lawrence, Massoud 1973). There are differences in drought resistance between the developmental stages in the same species. The first larval stage of Allacma fusca (L., 1758) is not resistant to drought whereas the later postembryonic stages are able to regulate their rates of water loss to some extent (Betsch, Vannier 1977). The same is true for the first larval stage of atmobiotic Collembola which lives in soil (e.g. some Entomobrya spp.) (Rusek 1964). Vannier (1983) deals with the different mechanisms of water exchange between a soil animal and the surrounding soil. He distinguish three basic types among Collembola regarding the adaptation to the edaphic environment:

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a) hydrophylic type includes forms which exhibit no control at all over their lost of body water (e.g. _Tetrodontophora bielanensis_ (Waga, 1942)).

b) mesophilic type includes species which exhibit a transpiration curve profile with a plateau indicating that the rate of body transpiration is maintained at a constant level independently of the reduction of internal water content (regulatory phenomenon, e.g. in _Tomocerus minor_ (Lubbock, 1962)).

c) the xerophilic (better: xerotolerant) type also can regulate its transpiration rate, but to a greater extent than the mesophilic type (e.g. _Seira domestica_ (Nicolet, 1841), _Allacma fusca_).

Ecomorphosis is a wide spread phenomenon in some collembolan families, especially in _Hypogastruridae_ and _Isotomidae_ (but also in some _Tullbergiinae_), and is related to increasing temperature and drought during spring and summer in xeric habitats. Ecomorphic animals have the ability to keep their water content at a certain level, but show a poorer water regulation (Dalens, Vannier 1979). Poinsot (1974) described anhydrobiosis in some xerotolerant species. Animals in anhydrobiosis lost about 65% of their total water content and endured the dry period in an inactive state. Anhydrobiosis is reversible and the animals become active when soil moisture rises. Testering (1981) described quiescence in some epigeic Collembola during which the animals starve and generally show a lower metabolic rate, including transpiration. Some of the euedaphic species very sensitive to dessication have developed an extensive water conducting system comparable with the terrestrial isopods (Rusek 1987). These species (e.g. _Isotomiella minor_ (Schäffer, 1896), _Oncopodura_ spp., _Megalothorax_ spp.) can compensate for water deficiency during the night when the dew point within the soil is reached.

In some ecosystems, such as flooded meadows and riparian forests, Collembola have to cope with a surplus of water. During the spring inundations, when water temperatures are low and oxygen content sufficiently high, they survive in inundated soil almost without damage,whereas during the summer flood collembolan density is reduced drastically (by 89%). The euedaphic forms are reduced more than the hemiedaphic and epigeic ones (Rusek 1984). Some species can survive the summer inundation in an egg stage and recolonize the soil soon after the water retreats with newly hatched animals (e.g. _Isotomiella minor_), others are completely destroyed and recolonization takes place from the surrounding higher elevation localities (e.g. _Folsomia quadrioculata_ (Tullberg, 1871)).

2.2. Temperature

As in most soil animals, the optimal temperature for Collembola is low and lies between 5 and 15°C. But there are species active at -2 or +28°C, also. Adaptation to very low temperatures is a well known phenomenon in some Collembola, especially species in polar and alpine zones. Overwintering species in the continental climatic regions of the temperate
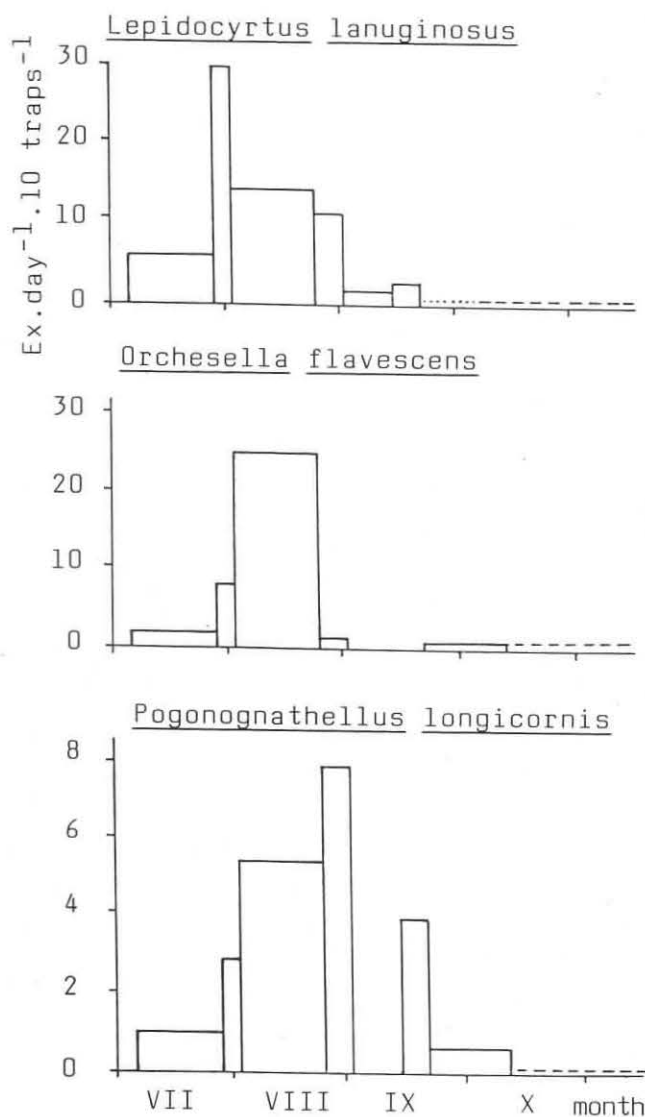
Fig. 1: Surface activity (columns) and hibernation (dashed line) of three epigeic species (South Bohemia, unpublished data).

zones can also develope adaptive mechanisms to tolerate very low temperature. The mechanisms by which this is achieved has been studied by many authors (Block 1980). Two groups can be distinguished in Collembola, as well as in other arthropods: freezing susceptable and freezing tolerant species. In the first group, the body fluids are maintained in a liquid state below the normal freezing point by the presence of polyhydric alcohols and sugars. The freezing tolerant species survive extracellular freezing by means of ice mucleators in the body. Glycerol plays an important role in these species in reducing cell damage. It is well known to synecologists that Collembola can be extracted from completely frozen soil samples taken during the winter. However soil temperatures below the snow cover can be up to $+5^{o}C$ or more, which is high enough for activity. There are many species of Collembola without cold resistance which die in the autumn and pass the winter in the egg stage. To this group belong epigeic and atmobiotic species of Smithuridae, Bourletiellidae, Dicyrtomidae, Entomobrya spp., Lepidocyrtus spp. and others. Since we can derive activity patterns from the soil surface studies (Fig. 1), it appears that some collembolan species found during the winter are in fact in hibernation and are inactive during the late autumn and winter (e.g. Lepidocyrtus lanuginosus (Gmelin, 1788), Pogonognathellus longicornis (Müller, 1776), Orchesella flavescens (Bourlet, 1839)). We have to assume the tropical

species will not tolerate temperatures near 0°C and probably have low-range stenothermic demands.

2.3. Soil chemical properties

The composition of the soil air differs from the atmospheric one. Solid soil particles slow down the gas diffusion between soil and atmosphere. CO_2 concentration in the atmospheric air is 0.03%, whereas in the soil it can reach 0.5% or even more. The concentration of CO_2 is heterogenous in the soil horizontally as well as vertically. In Folsomia candida (Willem, 1902) a positive reaction to a concentration gradient of CO_2 was established as in other soil animals (Klinger 1959) as an adaptation for food searching in microhabitats with higher biological activity in soil (i.e. CO_2 production by roots and soil organisms). Vannier (1983) discusses responses to CO_2 in acid and calcareous soils. In an acid soil, higher CO_2 concentrations can have a selective influence on the soil fauna, favouring species possessing adaptive mechanisms (reduction in metabolic level, autoregulation of the acid-base balance). It seems likely that such species are CO_2-independent. In acid soils Onychiurus armatus (Tullberg, 1869) tolerates CO_2 concentrations up to 35%, whereas for Onychiurus granulosus Stach, 1929 living in neutral or calcareous soils, even a 1.7% concentration is fatal. Atmobiotic and epigeic species are much more sensitive to CO_2 than species living deeper in the soil. Zinkler and Rüssbeck (1986) have demonstrated that some euedaphic Collembola may survive anoxia and described three different physiological adaptations to low oxygen concentrations.

There are many data about the impact of soil pH on Collembola (Hagvar 1987). Since Collembola have a waterrepellent integument, direct physiological effects are not considered. Artificial changes in the soil pH by simulated acid rain, or by liming, affected the population size of many edaphic collembolans. The results were supported by a laboratory experiment where the species were presented with sterile soil samples with different pH levels. Mesaphorura yosii (Rusek, 1967), Micranurida pygmaea Börner, 1901 and Willemia anophthalma Börner, 1901 were established as acidophilic and Isotoma notabilis Schäffer, 1896 as calciphilic. Hagvar (1987) confirmed these results by fieldstudies and presented eight hypotheses to explain the reaction of microarthropods to pH. Certain observations indicate that competition between different species may lead to a preference for a particular pH level. Comparing these data with results of other authors, in M. yosii, M. pygmaea and W. anophthalma acidophily was confirmed, whereas I. notabilis tends to be acidophilic, also, but less so (cf Ponge 1983).

Concerning the relation of Collembola to other soil chemical properties, such as C, N, Ca, Mg, Mn, Na, K content, etc., we have only a few data available in the literature. Studies by Hagvar and Abrahamsen (1984) have shown that Collembola cannot indicate the soil chemical properties as precisely as, can, for instance, certain plants. Combinations of species may,

however, increase the level of detection. The authors had two major problems in interpreting their results. First, several chemical soil parameters are intercorrelated. Also physical and biological parameters such as humus type, soil porosity and microfloral communities influence the soil chemistry. Secondly, mathematical correlations say nothing about causal relationships. Correlations found in the field should be supported by laboratory experiments. Ponge with collaborators (cf Poursin, Ponge 1984, Ponge 1983) use multivariate analysis of correspondences to establish relationships between certain species and defined soil properties (e.g. humus form). Such an analysis also has to be tested in a laboratory.

The impact of some pollutants (pesticides, heavy metals) on Collembola has been studied by many authors in the field as well as in the laboratory. Some Collembola can accumulate and excrete heavy metals in form of sphaerocrystals (Humbert 1977), but these polutants have a negative effect on the reproduction and metabolic rate (Joose, Verhoef 1983).

2.4. Food

Collembola are an extremely diversified group as regards food requirements. All species of the genus Friesea are predators feeding on soil Rotatoria, enchytraeids and free living nematodes. Metisotoma grandiceps (Reuter, 1891) feeds on other Collembola. The morphological adaptations of the collembolan mouth parts to different types of food are well known from the specialized literature. Alternatively Anderson and Healy (1972) considered soil Collembola as rather generalized feeders. Zachariae (1963) concluded incorrectly that Collembola do not play an important role in the disintegration of dead organic matter and in the process of formation of soil microstructure (Rusek 1985). He overemphasised the importance of surface dwelling species, producing soft or "fluid" excrements,in contradiction with existing data in the literature (Dunger 1956, Kubiena 1955). Zachariae's opinion was adopted by many pedological and soil biological authors and led to some misunderstanding of the role of Collembola in soil and ecosystems.

Three main approaches are applied in studies of food preferences of Collembola: a) gut content analysis, b) food preference experiments, c) analysis of gut microflora, followed by testing the food preference among species isolated from the gut and from the soil.

Fig. 2: Food preference of Onychiurus vanderdrifti to Penicillium spinulosum (circles) and P. nigricans.

The gut content analysis and the analysis of the gut microflora may lead to incorrect

interpretation because of the "ballast" eaten together with the main food. Some atmobiotic species are phytopagous and feed on live plant tissues, e.g. Sminthurus viridis L., 1758. Other species feed on pollen grains (e.g. Heterosminthurus spp., Bourletiella spp., Lepidocyrtus spp.), but some atmobiotic Symphypleona eat hyphae and spores of fungae and vary their food requirements (polen, algae, plant tissues) throughout the year (Nadtochiy 1987).

Many of the epigeic, hemiedaphic and euedaphic species belong to animals which mechanically degrade dead organic matter, including litter. It is known, the litter must be colonized and chemically altered by microflora before Collembola and other soil animals can use it as food (Dunger 1956). Most euedaphic and hemiedaphic species consume mycelium and spores of soil fungi and in many contributions is shown that certain species prefer a narrow spectrum of fungal species only (Mills, Sinha 1971). The food of the species with sucking mouthparts is not known, but we suppose the main constituents are bacterial cells and yeasts. The "rakes" and "brushes" on the maxillae of some species will serve as filters and for "sweeping" microorganisms from the substrate. Some epigeic species are algivorous (Nekrasova, Artemeva 1978). It was recorded by Matic and Koledin (1985) that Tetrodontophora bielanensis eat a different spectrum of fungi during the year according to the changes in the spectrum of fungi in the soil, but did not feed on bacteria, actinomycetes and other groups of soil microorganisms. When two or more species from the same locality use an identical food resource, its utilization usually differs. Kilbertus and Vannier (1979) have shown the hyphae in the excrements of Tomocerus minor are empty, whereas the fungivorous Alacma fusca digests the spores, and the hyphae remain intact. Orchesella villosa (Geoffroy, 1764) feeds mainly on soil algae. Orchesella cincta (L., 1758) feeds partly on algae, too, but the cell content is ingested only partially. The other food constituent of O. cincta is bacteria. Also the physiological stage of the soil microflora may influence the food preference. In our experiments Onychiurus vanderdrifti Gisin, 1952 preferred Penicillium spinulosum only in the first days of the experiment, later preference for this fungus species decreased, but it increased for Penicillium nigricans. On the fourth to fifth day the preference for both Penicillium species was almost the same and then it changed to P. nigricans (Fig. 2), reaching the highest values on the sixth to eighth day and then decreased. It is possible, that during fungal growth, increased metabolites repel the feeding animals.

Palatability of food depends on the enzymes in the gut. We have a few data concerning digestive enzymes in Collembola (e. g. Zinkler, Stecken 1987), but in the filled gut it is difficult to distinguish between enzymes produced by the animal alone and those of the microflora.

3. Synecology

It might seem that the growth in collembolan taxonomy during

Life forms:

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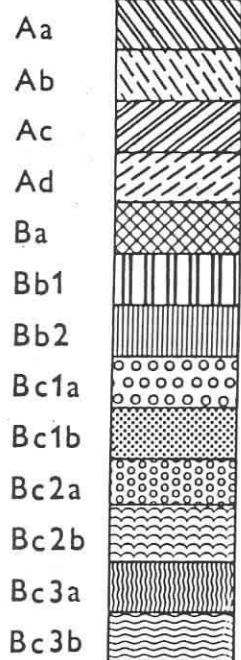Bb1
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Fig. 3: Collembolan life forms and their spectra in pioneer (102 - 106), advanced grassland communities (107 - 116), and climax oak forest (117 - 121). In white circles number of spp.(based on data in Kubíková, Rusek 1976).

the last 30 years has stimulated synecological studies. But it is not the case. The development of autecology and ecophysiology proceeded independently of taxonomy, because it was usually founded on the most common, sufficiently well defined species. Although the number of synecologically oriented contributions is not disproportionally low in comparison with autecological ones, they are of a different quality. Such contributions, which do not take into consideration the taxonomical progress, and where it is evident that the authors used older earlier publications for determination (e.g. Gisin 1960) or keys zoogeographically unsuitable for the given geographic area, are to be considered as worthless. In addition,

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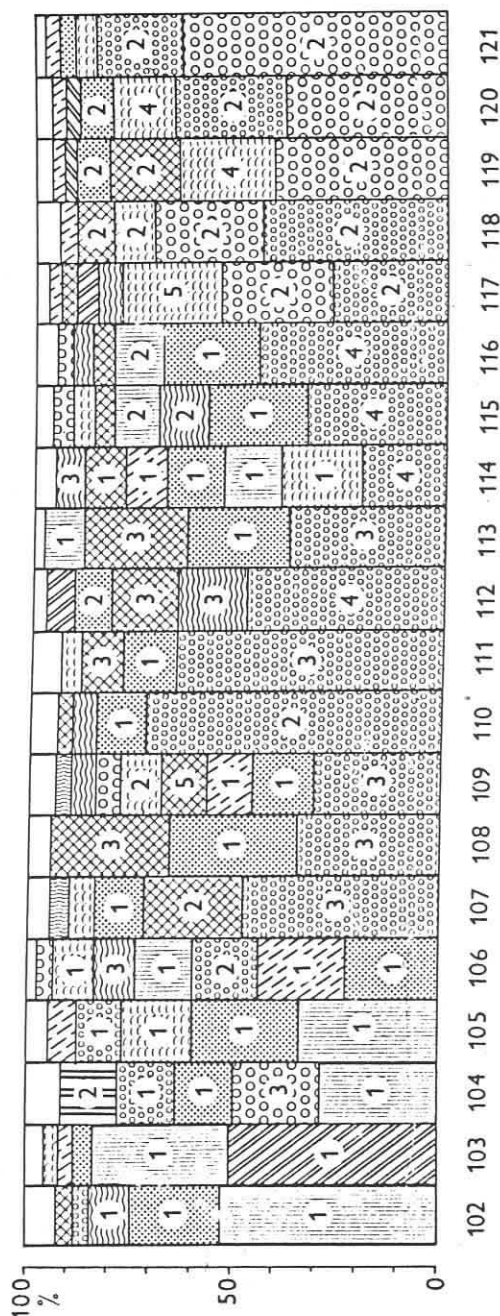
in many works like these, it is apparent that the authors did not master the determination as well as the methods for soil microarthropod studies.

The quality of synecological contributions is completely dependent on the taxonomical knowledge of the author. Contributions not only describing collembolan communities but explaining some ecological phenomena and contributing to general ecological theory are usually connected with well known taxonomical schools or taxonomists.

To support synecological research on Collembola it is necessary to do parallel taxonomical studies or to collaborate with a taxonomist to check the determination. For further progress in ecology we need new keys for determination written by the most experienced taxonomists.

For descriptions of collembolan communities basic as well as more complex parameters are used. Some authors applied very sophisticated mathematical methods to characterize and compare the established communities, but very often little taxonomical knowledge is evident from the list of species. On the other hand, there are also many valuable synecological contributions from different countries which are a base for further development in synecology and general ecology.

Conspicuous morphological differences among Collembola living in diverse habitats led Gisin (1943) to their classification into five groups of life forms, differing morphologically as well as ecologically. Gisin´s system of life forms was modified by Bockemühl (1956) and Stebajeva (1970). In all these modifications we can find shortcomings regarding disunited designation of morphological criteria, unfamiliarity with the true bionomy and ecology of the classified species and exaggerated effort to fix morphological criteria of each life form category regardless of phyletical trends in some families. For example, the number of ommatidia in the compound eyes was probably not the same in the ancestors of individual phyletical lines of Collembola, namely 8 + 8. The ancestors of Ony-chiurus were probably eyeless (no eyes have also dark pigmented species with well developed furca such as Tetrodontophora bielanensis and Lophognathella choreutes Börner, 1908), and those of Xenylla and related genera did not possess more than 5 + 5 ommatidia. But in the existing systems of life forms they were classified as euedaphic species. Therefore a new system of life forms for Collembola and Protura was proposed (Rusek, in press) as follows:

A. Atmobionts
   a) macrophytobionts; b) microphytobionts; c) xylobionts; d) neustonts;
B. Edaphobionts
   a) epigeonts; b) hemiedaphobionts - Bb1. upper, Bb2. lower; c) euedaphobions - Bc1. large (a - with furca, b - furca missing or reduced), Bc2. medium (a - with furca, b - furca missing or reduced), Bc3. small (a - with furca, b - furca missing or reduced) (Fig. 3).

The life form structure is an important parameter of collembolan communities and reflects, for example, the development stade during a succession (Fig. 3), can characterize the
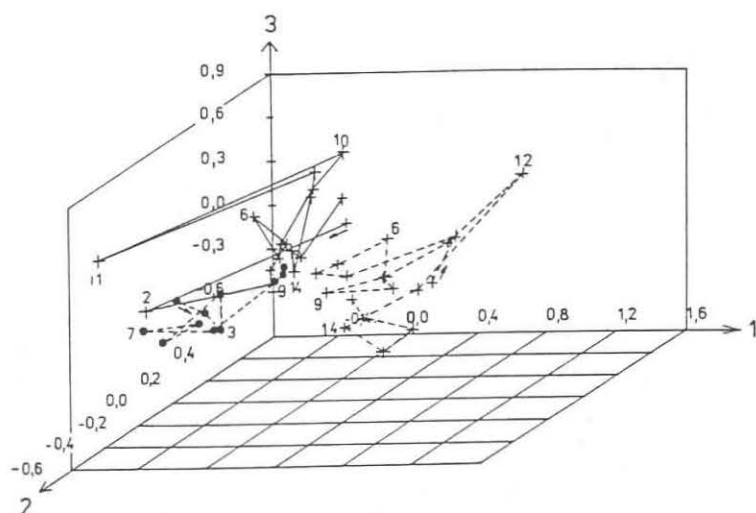
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Fig. 4: Ordination of samples from swampy (black dots), wet (full line) and dry (das - hed line) meadows. The inundations pushed the samples 2 and 11 from the wet meadow in the space of the swampy one (Rusek 1984).

soil microstru- cture, etc.(Ru- sek, in press). Samples from periods with extreme clima- tical conditi- ons are chan- ging their pa- rameters (Fig. 3, samples No. 103, 104, 109, 114) in connec- tion with the stade of suc- cessional de- velopment of the community. The changes are greater and ex- tended to lon- ger period in pioneer eco- systems (103, 104), less and shorter in du- ration in the more advanced ones, and almost missing in clima- xes (117 - 121). Some parameters of more advanced communities are in the extreme periods closer to or identical with the pa- rameters of the less developed successive stages, as demon- strated by ordination (Fig. 4).

Collembola are no doubt an excellent subject for synecolo- gical studies. But there is a barrier for further development due to the lack of recent literature for identification. Syne- cological contributions dealing with Collembola almost did not influence general ecology and ecological theories. Collembolo- gists are contributing in an unappropriately low level to the on-going large international projects and programmes (SCOPE, IGBP, MaB, etc.). Participation in such projects would stimu- late not only the synecology but also the taxonomy of Collem- bola.

4. Conclusion

A great progress in autecology and ecophysiology of Collem- bola was achieved in the last decades. The results are based on the studies of the most common species. Autecological rese- arch should be oriented in the future to a wider spectrum of species, especially to the dominant and wide-spread ones, playing a leading role in ecosystem functionning. Differences in ecophysiology among diverse life forms may elucidate bio- logy and ecological demands of related taxa as well as their phylogeny. Collembola are an important part of soil mesofauna. To stimulate further synecological studies new comprehensive works for determination are needed. Participation in large in-

ternational ecological programmes and projects is recommmended
to employ the results on a broad general ecological basis.

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